Lyria santoensis Ladd, spec. nov.

Figures *10, 11*: Holotype USNM 175138   × 1
Figure *12*: Same, apex   × 5
Figure *13*: Same, aperture   × 1½
Figures *14, 15*: Paratype USNM 175139   × 1

All specimens coated with ammonium chloride

Lyria Gray, 1847

Gray, 1847, Proc. Zool. Soc. London, 15: 141.

Type (by O. D.): *Voluta nucleus* Lamarck. Holocene, southwest Pacific.

Lyria mallicki Ladd, spec. nov.

Figures 2 to 9

Description: Medium in size, high-spired, slender. Protoconch of two smooth convex whorls, coiled at a slight angle to the axis of the spire, followed by seven sculptured whorls. Sculpture consisting of broad, rounded axial ribs, eighteen on penultimate whorl; base of body whorl with spiral grooves; suture distinct, made wavy by the wide axial ribs. Aperture slightly longer than remainder of spire; columella with three strong oblique plaits, posterior to which are about a dozen weak ridges, the last being a little stronger than the others; outer lip thickened. The three type specimens are larger than the other seven specimens and all of the three show traces of color pattern in the form of regularly-spaced spiral lines of reddish brown with irregular patches of the same color below the suture.

Measurements of the holotype, USNM 175096: height 48.0 mm, diameter 19.2 mm. from station SM242–386A. Paratype A, USNM 214226: height 45.7 mm, diameter 17.8 mm. from USGS sta. 25715. Paratype B from station SM 242 – 185 A is deposited in British Museum (Natural History), No. GG 19760. It measures: height 33.0 mm, diameter 15.5 mm.

Discussion: The New Hebrides fossil seems to have no close living relatives but may be compared to several described forms. It resembles *Lyria mitraeformis* Lamarck, a common Australian species, but is more slender, less strongly ribbed and has a sharper apex. In shape and gross ornamentation the fossil resembles *L. delessertiana* (Petit), a species living in the western Indian Ocean (Weaver & duPont, 1970: 17; plt. 4A, 4B) but that species is larger, has narrower, sharper and more numerous axial ribs, fewer whorls and a more extended and more heavily plaited columnar callus. *L. mallicki* also resembles *L. planicostata* Sowerby, a species known only from the type in the British Museum which was collected in an unknown locality (Weaver & duPont, 1970: 24, plt. 5K, 5L), but the New Hebrides fossil is more slender and has more numerous axial ribs.

Lyria mallicki is similar in many features to *L. jugosa* (J. de C. Sowerby), described from the early Miocene Gaj Beds of India (Sowerby, J. de C., 1840: plt. 26, fig. 25

and explanation) and later reported from several other horizons in the Late Tertiary and Pliocene-Pleistocene of Indonesia (Wanner & Hahn, 1935: 246; plt. 18, figs. 2-4; Beets, 1941: 119; plt. 6, figs. 253-254; Cox, 1948: 51; plt. 5, figs. 3a, b) but is more slender and its axial ribs lack the backward-projecting extremities of that species.

Lyria mallicki also resembles *L. hanzawai* MacNeil described from the Miocene of Okinawa (MacNeil, 1960: 98; plt. 9, fig. 7) but that species also has fewer axial ribs than *L. mallicki* and it shows no trace of spiral sculpture.

The species is named for Dr. D. I. J. Mallick of the New Hebrides Geological Survey who discovered the richly fossiliferous beds of Santo and made extensive collections of fossils from them.

Lyria santoensis Ladd, spec. nov.

(Figures 10 to 15)

Description: Shell large, elongate, strong. Protoconch of about two smooth, convex whorls, followed by nine gently convex whorls that make up a high, pointed teleoconch; suture slightly indented. Sculpture consisting of heavy axial ribs, twelve on the penultimate whorl; microscopic lines of growth, present over the entire shell, are bent forward at the suture; a few fine spirals are present near the base. Aperture narrow, exceeding half the length of the shell; inner lip with three-four strong anterior plaits and half a dozen smaller folds posteriorly; outer lip with a shallow depression within; siphonal notch moderately deep. Color pattern made up of spiral brown lines that, on the body whorl, are concentrated to make three wide brown bands, one at the base, one near the middle of the whorl and one at the suture.

Measurements, holotype, USNM 175138: length 87.7, diameter 29.6 mm, length of aperture 48.2 mm. paratype, USNM 175139: measures: length 78.6 mm, diameter 28.9 mm, length of aperture 45.6 mm.

Discussion: *Lyria santoensis* seems most clearly related to *L. lyraeformis* (Swainson), an even larger species (90 to 150 mm in length) living off the coast of Africa (Weaver & duPont, 1970: 21; plt. 5, figs. A, B; Aiken & Fuller, 1970: 15-16; plt. 7), but the fossil has more numerous whorls, fewer axial ribs and a more restricted spiral sculpture.

Occurrence: One complete and one fragmentary specimen from the Kere River near station SM242 and one specimen from the Navaka River, collected by Thomas Waller, John Bolango and Warren Blow, from boulders at the north end of the outcrop at station SM43 (USGS Cenozoic locality 25742).

ACKNOWLEDGMENTS

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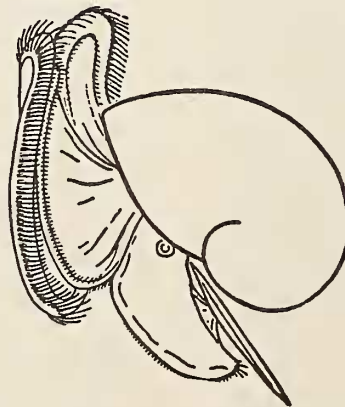
Feeding and the Radula in the Marine Pulmonate Limpet

Trimusculus reticulatus

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(1 Plate; 4 Text figures)

INTRODUCTION

THE MARINE PULMONATE limpet *Trimusculus reticulatus* is found on the west coast of North America. The first detailed in-life observations of a trimusculid limpet were made on this species by YONGE (1958). Particular attention was paid to the mantle cavity and some aspects of behaviour. Observations were also made on mucus secretion, the role of the large cephalic lobes, odontophore extrusion and the use of the radula in "effectively scraping fine encrusting vegetation from the surface of the rock." More recently two other species have been looked at in detail. These are the New Zealand *Gadinalea nivea* (WALSBY, MORTON, & CROXALL, 1973) and the Australian *Trimusculus (Gadinia) conica,* (HAVEN, 1973). The latter work is principally concerned with the reproduction and development of the brooded young. Some notes on feeding demonstrate that it "takes place while the animals are stationary" and whilst it is admitted that no evidence of feeding behaviour was obtained in the laboratory she claims circumstantially that food is obtained by grazing the small area in front of the shell, of diatoms and settled debris. Walsby *et al.* describe the feeding mechanism and ecology of *Gadinalea nivea* in which habit and habitat are closely related. Feeding involves the utilization of the water turbulence and the animal orientates to the predominant current. In its normal position it hangs upside down and lowers the shell so that the water current enters from behind. Lavish mucus is produced from glands of the mantle lip and the front and sides of the foot. Mucus secreted as a curtain in front of the head overlies the mantle and is ballooned out by the current. Particles of phytoplankton are trapped by the mucus curtain acting like a "fly paper" rather than a sieve. After inspection by the extended oral lobes the curtain may then be enclosed by a hood formed by these lobes and ingested by means of the protrusible odontophore.

On a brief visit to the Hopkins Marine Station, Pacific Grove, California, in July 1972 opportunity was taken for a complementary study in life of *Trimusculus reticulatus.* Preserved and living specimens were transferred to the Marine Research Laboratory, Leigh, New Zealand for comparison with *Gadinalea nivea* and of these 4 were kept alive for over a year and two for over two years.

Yonge's in life description of *Trimusculus reticulatus* was found to be comprehensively informative but my observations and conclusions varied with his over feeding and motility. Like *Gadinalea nivea* (WALSBY *et al*, 1973), *T. reticulatus* is a passive filter feeder trapping suspended particles from the sea water with secreted mucus, although the details of the food collection vary slightly. In this paper aspects of the habits and habitat are reappraised in the light of the filter feeding behaviour; factors which facilitate this and which would preclude grazing as a food collecting mechanism.

HABITAT

Like YONGE (1958) I also found *Trimusculus reticulatus* in large colonies on the under surfaces of large overhanging blocks, on cave roofs and on the upper surfaces of slanting crevices, in the intertidal zone on exposed shores. These were always sites of low light intensity extending to complete darkness. About 50 were found on the inside of the roof of a redundant sea-water system intake sump well. This well was normally open only by a bottom grating, to turbulent water exchange. The animals were in almost total darkness and the shells clean, uneroded and creamish white. Clearly any growth of attached photosynthetic diatoms was not possible. In the most illuminated sites where the animals were found, deep in open shore crevices, the shells were normally tainted a dull grey-green by algal growth. However algal growth can be considered to be

minimal in such sites and was never sufficiently marked to smooth over the delicate ribbing of the shells. Analysis of incident light and chlorophyll α concentrations from surface scrapings (WALSBY et al., 1973) show that in such dark places, even where there may be some tainting, available alga for grazers is negligible. This is reflected by the absence of recognized grazers in these sites. Animals associated with *T. reticulatus* were all known filter feeders; tube worms and barnacles. YONGE (1958) showed that like *Gadinalea*, (WALSBY et al., op. cit), *T. reticulatus* has poor cleansing ciliation, principally a narrow band conducting particles along the pallial groove on each side of the foot. It is therefore important that the animals inhabit a site free from sediment and this would help to explain why they are only found on the roofs of caves and under-surfaces. YONGE, (1953) suggested that *T. reticulatus* occupies much the same habitat as the sessile limpet *Hipponix antiquatus*. He has shown this animal to feed indiscriminately on large particles such as segments of calcareous algae that come within the very limited area of the front of the shell, by catching them with the active muscular proboscis and large distensible mouth, aided by the lateral terminal lobes flanking the mouth. Further observations on the relationship between *Hipponix* and *Trimusculus*, (YONGE, 1960) showed that whilst closely associated their precise habitats are quite distinct. An extreme storm which overturned massive blocks on the shore led Yonge to observe that *"T. reticulatus* is just as confined to the roof of these crevices as *Hipponix* is to the floor."* With habitat so clearly differentiated, albeit on a micro-scale, it is reasonable that habit should also be distinct.

ACTIVITY AND LOCOMOTION

YONGE (1958) described *Trimusculus reticulatus* as a mobile animal because it moved freely in aquaria before finally establishing position above the water line. However, apparently animals on the overturned blocks did not move and in this study *T. reticulatus,* whilst capable of movement in unnatural situations, has been found to be essentially sessile. One of the four animals studied in detail has not moved or changed orientation for nearly two years and the others after settling have remained immobile between experiments for up to seven months. Thus adults retain the ability to move efficiently but probably only rarely do so. This is quite reasonable as the same muscles are used in both locomotion and attachment. MILLER (1974) demonstrates that for maximum stationary tenacity shell length to foot length ratios of 1.5, together with foot length to foot width ratios of between 1.1 and 1.5, are optimal. It is interesting that in *T. reticulatus* these are 1.5 and 1.15 respectively, indicating excellent adaptation to the sessile habit.

In *Gadinalea* the adult shells are commonly misshapen through mutual lateral compression and marked jigsawing and even piling of two or three layers of animals, within a colony, results. This is generally less well marked in *Trimusculus reticulatus* but they are found closely aggregated, frequently show marginal shell conformity to the rock surface, and limited jigsawing and one example of piling was found. This must therefore preclude regular movement by the animals.

MUCUS SECRETION

When freshly collected I also found "great quantities of very viscous mucous, stringy and tenacious in quality" was secreted (YONGE, 1958). However this only occurred so long as the beasts remained unattached. From YONGE's drawing (1958: fig. 2) it may be seen, by the in-folding of the margins of the base of the foot that this study was made with the animal unattached. When the animals are attached, for example, to a glass or clear acrylic plate in-life examination is not impeded by copious mucus secretion.

Histological sections show that like *Gadinalea nivea, Trimusculus reticulatus* has a profusion of mucus glands over the mantle lip and also on the front of the foot and the latero-dorsal areas of the head. Under simulated natural conditions there appears to be a steady streaming of mucus which is collected by repeated odontophore protrusion and withdrawal when the animal is feeding. The steady mucus secretion may be effected by sustained or rhythmic contraction of the fine muscular trabeculae dividing the large mantle lip blood lacunae which radiate out across the mantle and can act as an incompressible hydrostatic skeleton behind the epithelial layer rich in mucus glands. In the foot these large blood spaces do not occur and the frontal epithelial mucus glands directly overlie the foot muscle. Presumably muscle ends reticulating between the mucus cells to the surface epithelia are able to exert an opposing steady compression force to exude mucus when the pedal muscle contracts against the substrate. When the animal is detached and the foot distorted through unnatural contraction, controlled secretion is lost and copious mucus secretion results.

THE ORAL HOOD AND MOUTH PARTS

Morphologically the oral hood is very similar to that of *Gadinalea nivea.* A clear mucus curtain characteristic of

G. nivea has not been observed nor the hood behaviour of scanning associated with its filtrant loading. Normally the hood is held within the confines of the shell. However, occasionally it has been observed to extend the oral lobes up to 3 mm beyond the shell margin with the tips of the lobes turned down over the shell margin, away from the substrate (the animal being naturally in the inverted position). Odontophore protrusion never occurs whilst the hood is so extended and whilst the function of this purposeful activity is uncertain, sensing of the water outside may be involved.

With the animal attached to a false transparent roof, appropriately sloped, odontophore protrusion may be readily observed during the feeding bursts. During such a burst the odontophore is protruded rhythmically about once per second and uninterrupted bursts have been observed to last as long as 20 minutes. This sustained activity is unlike that reported for any other gastropod while stationary and is more reminiscent of barnacle cirral feeding strokes. In the feeding position the mouth is a slit normally perpendicular to the substrate rather than one in the same plane and opposed to the substrate as in known grazers such as *Siphonaria*. Odontophore protrusion is forward with a terminating dorsal inflection away from the substrate which would preclude normal grazing activities but serve well to drag food-bearing mucus overlying the mantle lip and streaming off the foot, into the mouth.

Occasionally the oral lappets, which normally overlap slightly, are drawn apart and the odontophore protrusion directed towards the substrate before the upward inflection away from it. This falls far short of the grazing stroke of say, *Siphonaria zelandica* in which the mouth is opposed to the substrate and the grazing stroke, seen through a glass plate, runs the backwardly inflected tip of the radula along the surface. In *Gadinalea nivea* odontophore protrusion, to ingest the mucus curtain, occurs with the shell retracted to the substrate. This protrusion appears similar to that observed in *Trimusculus reticulatus* when not retracted. Further observations of *G. nivea* have shown that under conditions of decreased turbulence protrusion similar to that in *T. reticulatus* may occur though only for short bursts.

The odontophore is large and when withdrawn it is infolded and fully fills the buccal cavity. To observe it whole it is necessary to remove the buccal mass by dissection. The front of the foot is cut away to expose the ventral side of the head. A ventral incision is made to separate the oral lobes which are then trimmed away back to the mouth. The incision is continued back through the "neck" into the visceral mass. The lateral walls of the neck are trimmed and the antero-lateral pedal musculature cut away affording access to the buccal mass which may then be excised
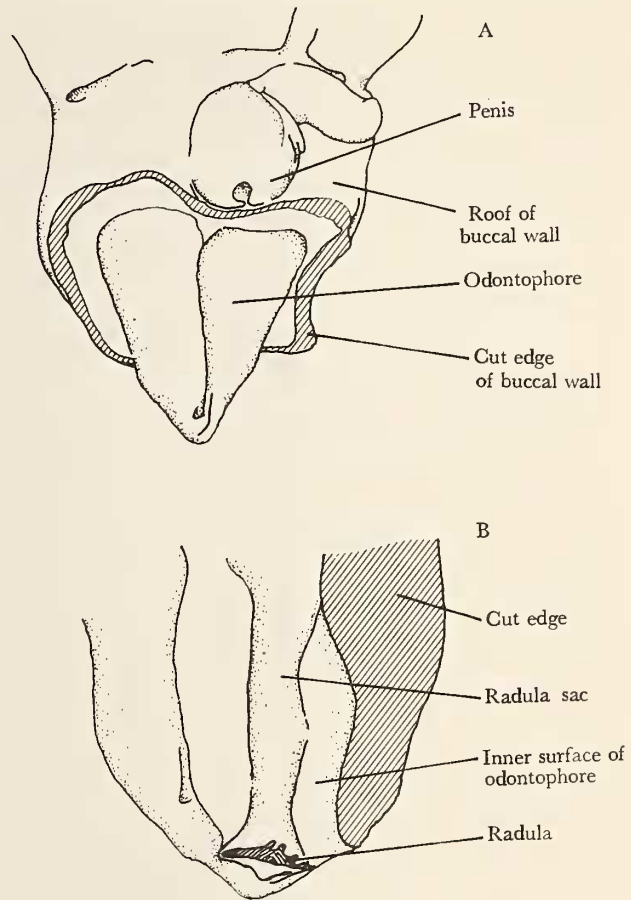

Figure 1

A. Excised buccal mass of *Trimusculus reticulatus* with front and side walls cut away to expose the odontophore

B. Odontophore with left infolded section cut away and the right infolded side inflected back to expose the odontophoral trough, radula sac and opening and the tip of the radula

entire. It is turned over and the lips and walls around the mouth cut away to expose the heart shaped proboscis (Figure 1A). The fleshy proboscis is infolded dorsally so that there is slight overlapping medially. The inner surface of the proboscis is inspected by cutting away one lateral infolded side and inflecting back the other. Along the floor lies a slightly raised tube which is the radula sac. It opens by a narrow window anteriorly, to expose the very tip of the radula (Figure 1B).

Both inner and outer surfaces of the proboscis are finely ridged. During proboscis eversion the floor is pushed out and up and the lateral infoldings open to flatten out the "U" shaped form of the withdrawn proboscis. Histological